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Fishing and the impact of marine reserves in a variable environment

Lynda D. Rodwell and Callum M. Roberts

Abstract: We use discrete-time models to investigate the impact of marine reserve establishment on fishery catch and biomass levels in open-access and quota-regulated fisheries under conditions of recruitment variability and natural mortality events. We find that under the conditions of variability tested, reserves can increase the probability of achieving target levels of biomass (60%, 35%, and 5% of carrying capacity) and can reduce catch variability in neighbouring fisheries, making future planning in the fishery more efficient. The size of the reserve required to meet each objective will depend on the initial condition of the stock and the exploitation rate in the fishery. Reserve coverage of between 20% and 40% prevent stock collapse in most cases. In heavily exploited fisheries, reserves are also likely to enhance mean catches, particularly in highly variable systems. If the stock has previously been heavily exploited, large reserves (≥60%) may be required to significantly increase the probability of achieving target biomass levels. However, once stocks have recovered, reserve coverage may be reduced without a reduction in this probability of success.

Résumé : Nous utilisons dans notre étude un modèle en temps discret pour étudier l'impact de l'établissement de réserves marines sur les captures de pêche et les niveaux de biomasse dans les pêches commerciales à accès libre et avec quota réglementé sous diverses conditions de variabilité du recrutement et d'événements de mortalité naturelle. Dans les conditions de variabilité testées, la présence de réserves peut permettre d'atteindre les valeurs de biomasse ciblées (60 %, 35 % et 5 % du stock limite) et elle peut réduire la variabilité des captures dans les pêches des régions avoisinantes, ce qui rend la planification de la pêche plus efficace. La taille de la réserve nécessaire pour atteindre chaque objectif dépend de la condition initiale du stock et du taux d'exploitation de la pêche. Dans la plupart des cas, une réserve qui représente entre 20 % et 40 % de la surface peut empêcher l'effondrement des stocks. Dans les pêches fortement exploitées, les réserves vont aussi vraisemblablement faire augmenter les captures moyennes, particulièrement dans les systèmes très variables. Si le stock a déjà été fortement exploité, il peut être nécessaire d'établir de grandes réserves (≥60 %) pour augmenter significativement la probabilité d'atteindre les niveaux de biomasses souhaités. Cependant, un fois les stocks rétablis, on peut réduire la surface de la réserve sans diminuer la probabilité de succès.

[Traduit par la Rédaction]

Introduction

The marine environment is highly variable. Some events are unpredictable, such as red tides, disease outbreaks, and seawater warming (Mann and Lazier 1996). Other events, often termed regime shifts, may be variable from year to year but follow some long-cycle underlying pattern (Steele 1998). These sources of variability and uncertainty pose serious problems for fisheries management (Mangel 2000*b*).

Managers make fish stock assessments at intervals and base recommendations for future catch limits. Changing environmental conditions that affect stock growth rates can render those predictions inaccurate, leading to over- or under-fishing, both of which carry economic costs. Adding to problems, capital invested during productive periods may not be easy to redeploy elsewhere as production levels fall. For example, year-to-year variation in the strength of upwelling in Peru drives the productivity of anchovy stocks. During strong El Niño conditions, upwelling virtually shuts down, greatly reducing productivity and concentrating remaining anchovy schools close to the coast (Longhurst and Pauly 1987). Stock assessments in the 1970s and 1980s failed to take upwelling strength into account. Continued high levels of fishing at a time of intense El Niño in the early 1970s drove the stock to collapse (Longhurst and Pauly 1987).

Regime shifts from cool to warm conditions in the North Pacific (Francis et al. 1998) and Atlantic Oceans (Alheit and Hagen 1997) drive underlying changes in productivity of fish stocks over decadal time scales. Stocks fluctuate from year-to-year against this background. While greater understanding of regime shifts can improve predictions of production levels, scientific sampling cannot remove or reduce

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stochastic variation. Consequently, fisheries management must operate with what have been termed "irreducible uncertainties" (Cohen 1966, 1967), making management error prone and risky. Marine reserves (i.e., areas that are permanently off limits to fishing) have been proposed as tools that can reduce the impact of uncertainty in fisheries management (Clark 1996; Lauck et al. 1998; Mangel 2000*a*). By protecting some fraction of fish stocks, it is argued that they increase the ability of managers to maintain target stock levels in the face of fluctuating productivity and to deliver less variable catches to the fishing industry. Using models, we explore these predictions for fisheries operating across a range of environmental variability and for different levels of management control.

There have been few attempts to model the effects of marine reserves that consider stochastic and variable events. Lauck et al. (1998) directly addressed the question of uncertainty and sustainability in fisheries management, focusing on irreducible scientific uncertainty. They used a simple model to explore the probability of maintaining a target population level under various scenarios of reserve size, levels of protection, and catch rates. They found that the chances of successfully maintaining 60% of the carrying capacity (an "Optimal Sustainable Population") over a 40-year time horizon fell dramatically when the total area available for exploitation exceeded 30%. An alternative to the reserve scenario would be to reduce catch rates to 10% of the stock level. They found that reserve protection can simultaneously achieve stock protection and a higher level of catch by intensifying fishing in the smaller fishing ground, but only at high levels of protection. They recommended marine reserves as a hedge against the prevailing uncertainties of biological, management, and economic systems.

Sumaila (1998) used a dynamic bioeconomic model to determine the optimal size of a marine reserve for the Barents Sea cod fishery with respect to economic rent, catches, and standing stock. Variability focused on recruitment failure events. That author found that reserves will only be bioeconomically beneficial when both transfer rates between protected and unprotected regions are high and the reserves are large. However, reserves increased biomass under all circumstances. The findings fully supported those of Lauck et al. (1998), who found that reserves hedge against biological losses. However, no consideration of the influence of reserve size on transfer rate was made. Furthermore, the model was developed in a way to suggest that the productivity of the stock increased with the size of the reserve. This may explain why it concluded that large reserves are necessary.

Mangel (2000*a*) developed stochastic methods to determine how much habitat needs to be set aside as reserve, once reserve objectives are decided. In this model, stochastic calculations are based on the harvest fraction being a random variable. "Persistence" of the stock is characterized by the probability that the stock stays above a critical level (35% or 60% of carrying capacity). Mangel found that reserves provided a buffer that increased the chances of sustainability of the stock and may not necessarily reduce harvest. He concluded that the fraction of management area that should be allocated to reserves will depend on biological, economic, and social conditions. In a second paper, Mangel (2000*b*) developed a model for a marine reserve for an open population subject to environmental uncertainty where natural mortality was a correlated random process, fishing mortality fluctuated, and recruitment was episodic. Catch was calculated as a fraction of the fish that disappeared each year (the rest attributed to natural mortality). Recruitment was episodic. The probability of maintaining the population at a level at or above 35% of carrying capacity was calculated. Probabilities were also calculated as a function of the fraction of habitat protected. Smaller reserves led to larger but more variable catches (i.e., there was a mean–variance trade-off). In this study, Mangel predicted that implementing a reserve will not increase catch but will decrease variability in catch and so help avoid boom and bust fishery cycles (e.g., Clark 1990).

In his stochastic model, Conrad (1999) introduced a linear total allowable catch function and presumed that fishery managers can measure biomass and can enforce the total allowable catch regulation. He introduced a random variable that influenced the growth of the fish stock. He found that through the movement process, biomass variability can be lower with a reserve of 40%–60% of the original grounds compared with the no-reserve case.

Each of these studies has addressed the variability of the marine environment and exploitation of marine resources in different ways. In this paper, we use discrete-time models to investigate the impact of marine reserve establishment in two contrasting fishery regimes: an otherwise open-access fishery and a regulated fishery (regulated by total allowable catch (TAC) quotas). Impacts of reserve establishment on fishery catch and biomass levels under conditions of both recruitment variability and natural mortality events are explored. Our aim is to assess the potential contribution of marine reserves to managing fisheries in variable environments. We will address the questions can marine reserves (*i*) increase probability of maintaining target biomass levels in the fishery, (*ii*) enhance mean catches over a given time period, and (*iii*) reduce the variability of catches in the fishery? For each question, we compare results of the open-access regime with the quota regime. We examine these questions in the context of both a previously unexploited fish stock (initially at carrying capacity) and a heavily exploited stock (initially one fifth of carrying capacity) facing varying levels of recruitment and natural mortality variability.

We compare the results of a highly variable system with those of a system where natural mortality and recruitment are deterministic. The highly variable system experiences stochastic recruitment with underlying regime shifts and stochastic natural mortality, with pulses representing catastrophic events such as disease or red tides. We examine the role of reserves in achieving stated management objectives, such as increasing the probability of total biomass remaining above target levels 60%, 35%, and 5% of carrying capacity for at least 25%, 50%, and 100% of the time, respectively, enhancing mean catches and reducing the variability of catches. We also consider how large an area should be protected to achieve these objectives. We do not consider explicit random exploitation functions but rather that exploitation is variable because of variability in the stock level and, in the open-access case, because of changing fishing effort. Results for both the open-access and quota-regulated fishery regimes are compared and contrasted.

Methods

The general models

We chose to examine the role of marine reserves in both the open-access fishery regime and the quota-regulated fishery to compare the outcome of variable effort and fixed effort regimes. These two regimes may approximate to a fishery with relative ease of entry and exit such as a low cost fishery and a commercial fishery regulated by strict quotas, respectively.

An open-access fishery

The conditions for open access are met when rents in the fishery are dissipated (i.e., profits are reduced to zero)

$$\pi_t = pH_t - cE_t = 0$$

where p is a unit price, H_t is the catch, c is a unit cost of fishing effort, E_t is fishing effort, and π_t is profit in time period t. E_t responds to profit levels in a previous time period. The change in effort is expressed as a function of profits in time period t and an effort adjustment parameter, ϕ, which reflects the ease of exit or entry to the industry (eq. 2).

Complete open access

The system of open access in the whole fishery is described by the two dynamic equations:

$$(1) \qquad X_{t+1} - X_t = -nX_t + R_t - H_t$$

$$(2) \qquad E_{t+1} - E_t = \phi(pH_t - cE_t)$$

where the growth of the stock is described by a spawner–recruit relationship. R_t is the recruitment (a function of biomass X_t) and n is natural mortality expressed as a proportion of total biomass (X_t). Equation 1 describes a biomass-dynamic relationship in which a change in X accounts for a change in both the number and size of individual fish.

Equilibrium is reached when $X_{t+1} - X_t = 0$ and $E_{t+1} - E_t = 0$. Using a Gordon–Schaefer catch function, $H_t = qE_tX_t$, where q is the catchability coefficient, the equilibrium biomass is $X^* = c/qp$.

Marine reserve and open access (in remaining fishing grounds)

The stock now is composed of two distinct substocks, X_1 and X_2, which occupy the reserve (proportion of management area, α) and the fishing grounds (proportion of management area, $1 - \alpha$), respectively. Though for modelling simplicity we specify two areas (i.e., a marine reserve and a fishing ground), the "reserve" corresponds to coverage of the management area with areas that are permanently off limits to fishing. That is, it represents a network of reserves covering a proportion of a management area rather than just one marine reserve. As the reserve is fully protected from fishing, there is only catch from the fishing grounds (H_2). The dynamics between the reserve and the fishing grounds are described by the transfer of recruits due to larval dispersal (T) and the movement of fish (M). T and M can be positive or negative depending on the relative biomasses inside and outside of the reserve and so represent movement in or out of the reserve.

The system with a reserve and a fishing ground is expressed by three dynamic equations:

$$(3) \qquad X_{1,t+1} - X_{1,t} = -n_1X_{1,t} + R_{1,t} - M_t - T_t$$

$$(4) \qquad X_{2,t+1} - X_{2,t} = -n_2X_{2,t} + R_{2,t} - H_{2,t} + M_t + T_t$$

$$(5) \qquad E_{2,t+1} - E_{2,t} = \phi(pH_{2,t} - cE_{2,t})$$

where the recruitment functions $R_{1,t}$ and $R_{2,t}$ are based on the Beverton–Holt recruitment function (Beverton and Holt 1957).

Equilibrium is reached when $X_{1,t+1} - X_{1,t} = 0$, $X_{2,t+1} - X_{2,t} = 0$, and $E_{2,t+1} - E_{2,t} = 0$. The Gordon–Schaefer function in this case is $H_{2,t} = qE_{2,t}X_{2,t}$, and so equilibrium biomass is $X_2^* = c/qp$. Therefore, the equilibrium level of biomass in the fishing ground (not total biomass) will be the same with or without reserve if costs, prices, and catchability are unchanged. n_1 and n_2 represent natural mortality in the reserve and fishing ground, respectively. These may reflect differences in stock composition or habitat quality in the two areas (Rodwell et al. 2003).

A quota-regulated fishery

In this case, we consider a fishery that has an imposed TAC quota policy. The quota is set as a fixed proportion of available fish biomass (i.e., a fixed exploitation rate) in the fishing ground (similar to the linear production function of Conrad (1999) and equivalent to the model used in Rodwell et al. (2002, 2003)).

Quota-regulated fishery without a reserve

This model can simply be expressed in terms of the catch function, which, if a linear catch quota, can be written as

$$(6) \qquad H = uX_t$$

where u represents a fixed exploitation rate or the total allowable proportion of biomass to be extracted subject to stock dynamics in eq. 1, ($X_{t+1} - X_t = -nX_t + R_t - H_t$).

Quota-regulated fishery with a reserve

In this case, the model is simply expressed using the catch function

$$(7) \qquad H_{2,t} = uX_{2,t}$$

subject to stock dynamics in eqs. 3 and 4 ($X_{1,t+1} - X_{1,t} = -n_1X_{1,t} + R_{1,t} - M_t - T_t$ and $X_{2,t+1} - X_{2,t} = -n_2X_{2,t} - H_{2,t} + R_{2,t} + M_t + T_t$, respectively).

Functional forms

Using the two formulations of the model, we can examine the impact of reserve establishment on biomass and catch levels and variability over a given time horizon. However, we must first specify the functional forms for movement of adult and juvenile fish (M) and transfer of recruits (T). The movement functions are the same as those used by Rodwell et al. (2002, 2003).

Fish movement, M_t

The movement of fish between the reserve and the fishing ground is a function of the biomasses in the two areas.

$$M_t = \sigma[(1-\alpha)X_1 - \alpha X_2] \tag{8}$$

where σ is the mobility coefficient of fish and $0 \le \sigma \le 1$. If $\sigma = 0$, fish are assumed to be sedentary; if $\sigma = 1$, fish are highly mobile. Equation 8 is equivalent to

$$M_t = \sigma A\alpha(1-\alpha)[X_1/A\alpha - X_2/A(1-\alpha)]$$

where A represents the management area, and α represents reserve coverage (the proportion of management area protected) (see Rodwell et al. 2002 for full explanation). Note that if $X_1/A\alpha > X_2/A(1-\alpha)$, then M is positive and fish move out of the reserve. If $X_1/A\alpha < X_2/A(1-\alpha)$, then M is negative and fish move into the reserve.

Recruit transfer, T_t

Larval movement patterns are taken as a function of the larval retention factor, θ. The recruit transfer function is given by

$$T_t = (1-\theta)[(1-\alpha)R_{1,t} - \alpha R_{2,t}] \quad \text{for } 0 \le \theta \le 1 \tag{9}$$

where θ is the proportion of larvae retained. If $\theta = 0$, then there is no larval retention and the larvae disperse uniformly. If $\theta = 1$, then full retention of larvae occurs. This results in no transfer of recruits between the reserve and the fishing ground.

The recruitment functions R_t, $R_{1,t}$, and $R_{2,t}$ are based on the Beverton–Holt recruitment function (Beverton and Holt 1957). However, they take different forms depending on the level of variability in the marine environment. These are described in detail in the Methods section.

Simulations

The models were set up with the two cases of recruitment and natural mortality variability described below. In each case, fish biomass and catch levels were considered for both the reserve and no-reserve cases.

Biomass analysis

In the biomass analysis, three biomass management objectives were stated, and the probability of achieving each of them were evaluated under the different fishery regimes and with reserve coverage ranging from 0% to 100%. The three objectives were (*i*) to maintain the stock at 60% of carrying capacity at least 25% of the time, (*ii*) to maintain the stock at 35% of carrying capacity at least 50% of the time, and (*iii*) to maintain the stock at 5% of carrying capacity 100% of the time.

These levels were chosen based on the recommendations that stocks should be kept at (*i*) 60% of carrying capacity — an economically optimal level of biomass (Lauck et al. 1998), (*ii*) 35% of carrying capacity — a level of biomass sufficient to prevent recruitment overfishing (in most cases) (Mangel 2000*b*), and (*iii*) 5% of carrying capacity, representing likely stock collapse.

The percentage of time for which the target level is to be achieved is a little more arbitrary. In a highly variable system to achieve an economic optimum, 100% is unlikely, whereas 25% of the time may be realistic and achievable. Maintaining the stock at 35% of carrying capacity at least 50% of the time also seems realistic. 5% carrying capacity 100% of the time is necessary to guarantee that the stock will not collapse.

The probability that the objective will be reached, in the variable system, is based on 200 runs of the model. In each run, the number of years the target biomass is reached is calculated and then the proportion of runs in which the objective is achieved forms the basis of the probability of success. In the deterministic system, there is just one run for which the target biomass objective is either achieved or not, so the probability is either 0 or 1.

Catch analysis

The catch objectives for management in this case were stated as (*i*) to increase mean catches over the management time horizon and (*ii*) to reduce catch variability over the management time horizon. Each scenario tested was evaluated on the criteria of meeting these objectives. Catch variability was measured in terms of standard deviation and also percentage variability (SD/mean catch × 100).

The findings of Rodwell et al. (2003) suggest that the impact of marine reserves on a fishery may be highly dependent on the condition of the stock at the time of reserve establishment. We therefore consider two contrasting initial stock conditions. The first is the case where the stock is initially at its carrying capacity and has high reproductive capacity, consistent with not having been previously exploited. The second illustrates the case when the stock is initially one fifth of its carrying capacity and low reproductive capacity consistent with previous heavy exploitation.

Cases of variability

We modelled the cases of a deterministic and a highly variable system to determine whether they would produce any significantly different outcomes in terms of the contributions of reserves to the fishery management objectives.

Deterministic system

For the case of deterministic and stable recruitment, the Beverton–Holt recruit production function for the reserve is

$$R_{1,t} = \frac{\varepsilon_1 X_{1,t}}{\gamma_1 \varepsilon_1 X_{1,t} + \beta_1} \tag{10}$$

where $R_{1,t}$ is recruit production of the reserve fish stock in time period t, $X_{1,t}$ is reserve fish biomass in time period t, γ_1 and β_1 are recruitment parameter estimates for the reserve stock for a given initial growth rate, and ε_1 is the proportion of the reserve stock that is reproductively mature. ε_1 will vary with time since protection (i.e., $\varepsilon_1 = f(t)$). $\varepsilon_1 X_1$ is taken as a proxy for spawning stock biomass in the reserve.

For the fishing ground stock, the Beverton–Holt recruit production function is

$$R_{2,t} = \frac{\varepsilon_2(X_{2,t} - \psi H_{2,t})}{\gamma_2 \varepsilon_2(X_{2,t} - \psi H_{2,t}) + \beta_2} \tag{11}$$

where ε_2 is the proportion of the fishing ground stock that is reproductively mature. This is a function of the exploitation rate in the fishing ground (i.e., $\varepsilon_2 = f(u)$ in the quota fishery, or $\varepsilon_2 = f(qE)$ in the open-access fishery). ψ is the proportion of exploitation taking place before recruitment (i.e., $0 \le \psi \le 1$). The only spawners are those remaining after a proportion of catch takes place (i.e., $\varepsilon_2(X_2 - \psi H_2)$) in each time period where $0 \le \psi \le 1$. See Rodwell et al. (2002) for discussion. The equivalent recruit production function for the no-reserve case is

$$R_t = \frac{\varepsilon(X_t - \psi H_t)}{\gamma\varepsilon(X_t - \psi H_t) + \beta}$$

Natural mortality is assumed to be a constant proportion of biomass.

Stochastic system

Recruitment is stochastic with underlying regime shifts

If recruitment is stochastic against a background of regime shifts, the functions are given by eqs. 12 and 13

$$(12) \qquad R_{1,t} = z_1 \exp(w_1)\left(\frac{\varepsilon_1 X_{1,t}}{\gamma_1\varepsilon_1 X_{1,t} + \beta_1}\right)$$

$$(13) \qquad R_{2,t} = z_2 \exp(w_2)\left[\frac{\varepsilon_2(X_{2,t} - \psi H_t)}{\gamma_2\varepsilon_2(X_{2,t} - \psi H_t) + \beta_2}\right]$$

where w_i is a random normal variable and so the errors have a lognormal distribution (Hilborn and Walters 1992). We take $w = w_1 = w_2$ (i.e., the reserve and the fishing ground face the same stochastic events) so that the true effects of the reserve can be determined. However, in reality different w values could represent spatial heterogeneity between reserve and fishing ground, reflecting better or worse conditions for recruitment. z_i represents the regime shift following a sine motion

$$(14) \qquad z_{i,t} = g_i + d_i \sin(tl_i)$$

where g_i is a constant, d_i is the depth of the phase, l_i is the length of the phase for area i where i = 1, 2 (reserve and fishing ground). Note that we take $z = z_1 = z_2$ for comparability between reserve and no-reserve results. The combination of the stochastic element ($\exp(w)$) and the underlying regime shift (z) is illustrated (Fig. 1*a*). This pattern of regime shifts illustrated is for $g_i = 1$, $d_i = 0.2$, and $l_i = 0.2$ and $-0.2 < w_i < 0.2$, with a mean of $w = 0$ (i.e., $\exp(w) = 1$). This is the underlying random process for all the simulations. The equivalent recruit production function for the no-reserve case is

$$R_t = z \exp(w)\frac{\varepsilon(X_t - \psi H_t)}{\gamma\varepsilon(X_t - \psi H_t) + \beta}$$

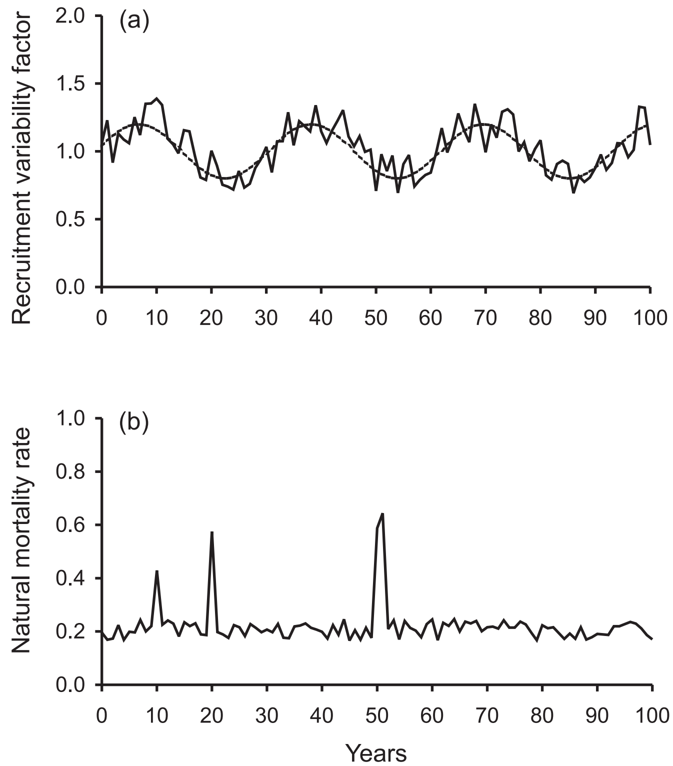
Natural mortality is stochastic with pulses

We also consider that natural mortality is likely to experience random fluctuations as well as sudden pulses brought about by disease or other natural events such as red tides, storms, and regional anoxia (i.e., a highly variable system). The general equation including a pulse is given by eq. 15, where n_0 is the base level of natural mortality, a random normal variable.

$$(15) \qquad n = \exp(n_0 + [\text{pulse}(\text{year, duration})] \times \text{intensity}$$

The natural mortality pulses (represented in Fig. 1*b*) were set up as shown in eqs. 16 and 17.

Fig. 1. (*a*) Recruitment variability factor ($z \exp(w)$) indicating an underlying regime shift (broken line) and stochastic fluctuations following a lognormal distribution (solid line). (*b*) Natural mortality variability indicated by stochastic fluctuation about a base level of 0.2, with pulses representing catastrophic mortality events.



$$(16) \qquad n = \exp(n_0) + [\text{pulse}(10,1)]0.3 + [\text{pulse}(20,1) + \text{pulse}(50,20)]0.5$$

$$(17) \qquad n_0 = \text{random normal}(-1.8,-1.4,-1.6, s)$$

where n is the proportion of biomass dying naturally each year, and s is the noise seed that varies for each simulation run. –1.8, –1.4, and –1.6 are the minimum, maximum, and mean values used in the random normal distribution, respectively. They approximate to a natural mortality rate between 0.16 and 0.24 and a mean of 0.2. The function represents a base natural mortality of 0.2 (20% per annum), with sudden pulses in years 10, 20, and 50 for 1-, 1-, and 2-year periods, respectively, at intensities of 0.3, 0.5, and 0.5, increasing natural mortality to 0.5, 0.7, and 0.7, respectively (50%, 70%, and 70%). Note that $n = n_1 = n_2$ (i.e., all stocks whether protected or unprotected are assumed to be subject to same natural mortality pulses).

Life history and fishery model parameters

Two scenarios of initial stock condition were tested: one where the stock was previously unexploited and another where the stock was previously heavily exploited. This was done to determine whether different management strategies are appropriate in each case. The growth patterns of both the previously unexploited stock and the previously heavily exploited stocks for the two cases of variability under the scenario of zero exploitation are illustrated (Fig. 2). Note that we do not specify units, since this is a simulation exercise to compare with and without reserve scenarios.

Previously unexploited stock

In this case, the initial total biomass level is set at X_1 = 2000 where carrying capacity of the stock is also 2000 (i.e., X_c = 2000). Hence $X_{1,0} = 2000\alpha$ and $X_{2,0} = 2000(1 - \alpha)$. In the open-access regime, $\pi_0 = 1000$ and $\phi = 0.01$. Therefore $E_{2,0} = E_0 = 10$. The growth parameters used are n_1, n_2, $n = 0.2$ (deterministic only); β_1, β_2, $\beta = 0.1$; $\varepsilon_1 = 0.7$; ε_2, $\varepsilon = 0.7\exp(-3u)$; $\gamma = 0.00243$; $\gamma_1 = 0.00243/\alpha$; $\gamma_2 = 0.00243/(1 - \alpha)$.

Previously heavily exploited stock

In this case, the initial total biomass level is set at X_1 = 400 in each scenario — one fifth of the carrying capacity X_c = 2000. Hence $X_{1,0} = 400\alpha$ and $X_{2,0} = 400(1 - \alpha)$. π_0 = 1000 and $\phi = 0.01$. Therefore $E_{2,0} = E_0 = 10$. The growth parameters used are n_1, n_2, $n = 0.2$ (deterministic only); β_1, β_2, $\beta = 0.3$ (the choice of β influences the time taken to return to carrying capacity); $\varepsilon_1 = 0.20+0.05t$ (for t = 0 to 10) and 0.7 (for t = 11 to 100) (we assume the reproductive capacity of stock at carrying capacity is 0.7, and it takes 10 years of protection for the stock to reach this level; see Rodwell et al. 2003); ε_2, $\varepsilon = 0.2\exp(-3u)$; $\gamma = 0.00229$; $\gamma_1 = 0.00229/\alpha$; $\gamma_2 = 0.00229/(1 - \alpha)$. Note from this that we assume that heavy exploitation affects recruitment rather than natural mortality, since exploitation reduces the average size of individual fish and so their fecundity. We also assume that the reproductive capacity of the stock continues to decline after heavy exploitation even if exploitation is reduced to a TAC of 10%, because even low levels of exploitation will result in the removal of the largest and most fecund fish, reducing overall reproductive capacity of the stock.

In both scenarios, the following parameters were used: $\sigma = 0.2$ (moderate fish movement); $\theta = 0.5$ (50% larval retention); $\psi = 1$ (all exploitation before spawning); g_1, g_2, $g = 1$; d_1, d_2, $d = 0.2$; l_1, l_2, $l = 0.2$; $u = 0.1$ to 0.5; $p = 0.2$; and c = 0.1. Reserves covering 0%, 20%, 40%, 60%, 80%, and 100% of the management area were tested (i.e., α = 0, 0.2, 0.4, 0.6, 0.8, and 1, respectively).

The simulation software package Vensim DSS® was used for the simulations. Simulations were run over a 120-year time horizon with a time step of 1 year. The first 20 years were taken as an adjustment period and the years 21–120 were analysed. We then compared results to the 1- to 100-year period. 200 runs were simulated with different levels of noise in each (noise seed s is a random variable).

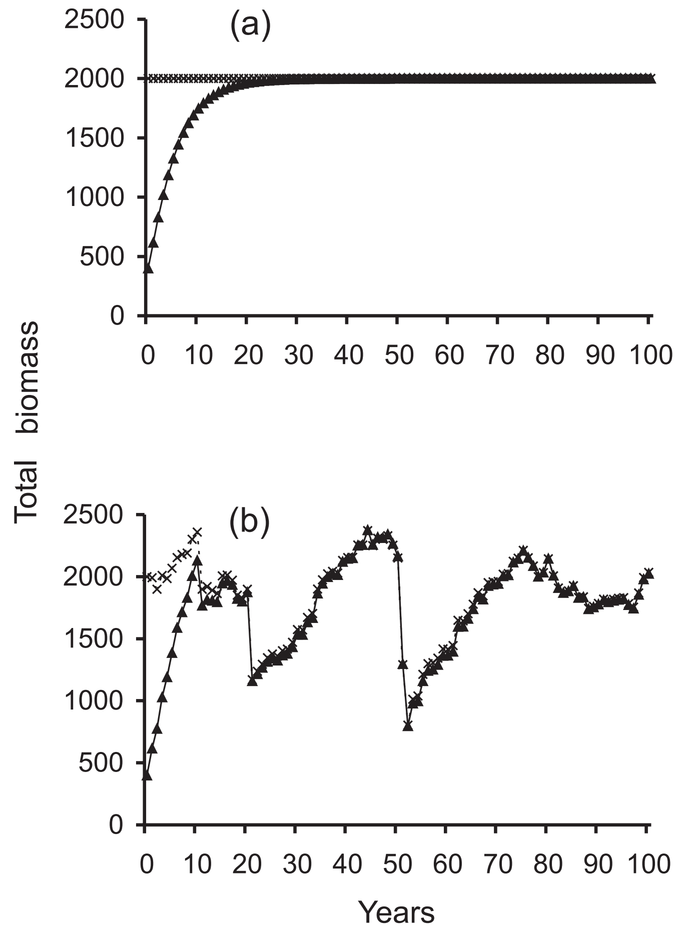
Results

Impacts on biomass

What is the impact of reserve establishment on total biomass levels?

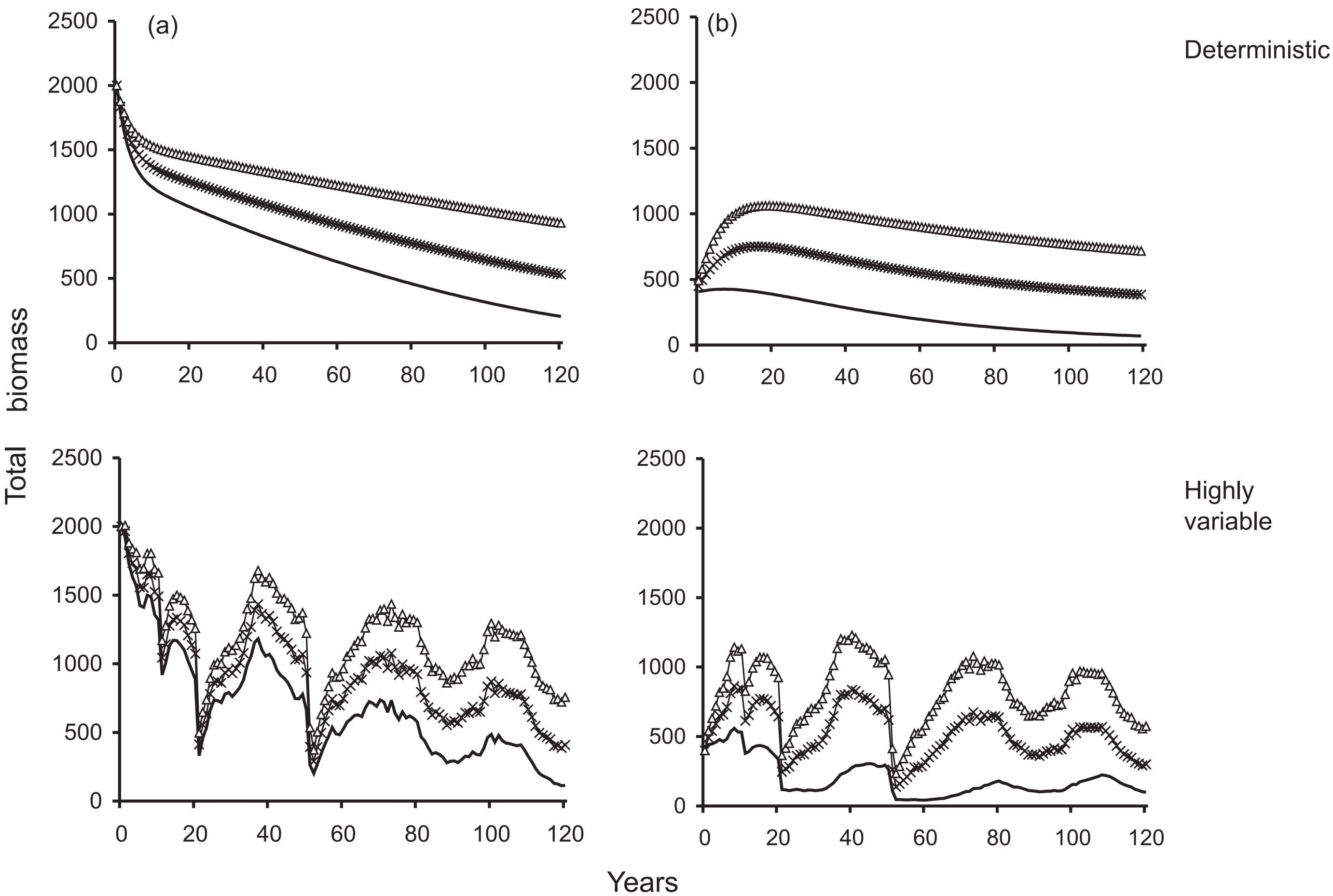
One main objective of establishing marine protected areas may be to allow stocks to recover or rebuild. In an open-access fishery, total biomass in both deterministic and highly variable marine systems is enhanced by a reserve whether the stock was previously unexploited or heavily exploited. The larger the reserve, the greater the biomass level (Fig. 3). The graphs compare the case of no-reserve against those of 20% and 40% reserve coverage (given the 20%–40% range of recommendations for reserve coverage suggested to maximize fishery benefits in Roberts and Hawkins (2000), NRC (2001), and Gell and Roberts (2003)). In the case of previous heavy exploitation and a highly variable system (Fig. 3b), the presence of a reserve covering 20% or 40% of the management area appears to prevent the stock plummeting to near zero levels. Note that over a longer time period, the biomass levels stabilize.

Fig. 2. Growth scenarios for previously unexploited stock (×) and previously heavily exploited stock (▲) in (a) a deterministic system and (b) a highly variable system for the scenario of zero exploitation. The carrying capacity of the stock is 2000 in each case.



In a TAC-regulated fishery, total biomass levels are also always higher with a reserve (Fig. 4 shows biomass levels with a TAC of 10%, 30%, 50%), and the larger the reserve, the higher the biomass. Total biomass levels also decrease with an increase in the quota level. However, without a reserve and in a previously heavily exploited fishery, the stock will collapse if the TAC reaches 20% or above (Fig. 4b). In a previously unexploited stock, total biomass levels will fall from the initial level with the imposition of a quota fishery with or without a reserve (Fig. 4a shows the results of one sample run). At low levels of exploitation (TAC 10%), the difference between biomass levels with and without reserve are small (with a mean level of 1243 without reserve and 1467 with a 40% reserve). The differences in biomass are, however, considerable at TAC 50% (with a mean level of 70 without a reserve and 702 with a 40% reserve). In a previously heavily exploited stock with a TAC of 50%, a reserve

Fig. 3. Total biomass levels in an open-access fishery for two stocks: (*a*) previously unexploited and (*b*) previously heavily exploited. No reserve (solid line), 20% reserve (×), and 40% reserve coverage (△) are shown in deterministic and highly variable systems. The figures for the highly variable case represent one sample run (out of 200 runs).



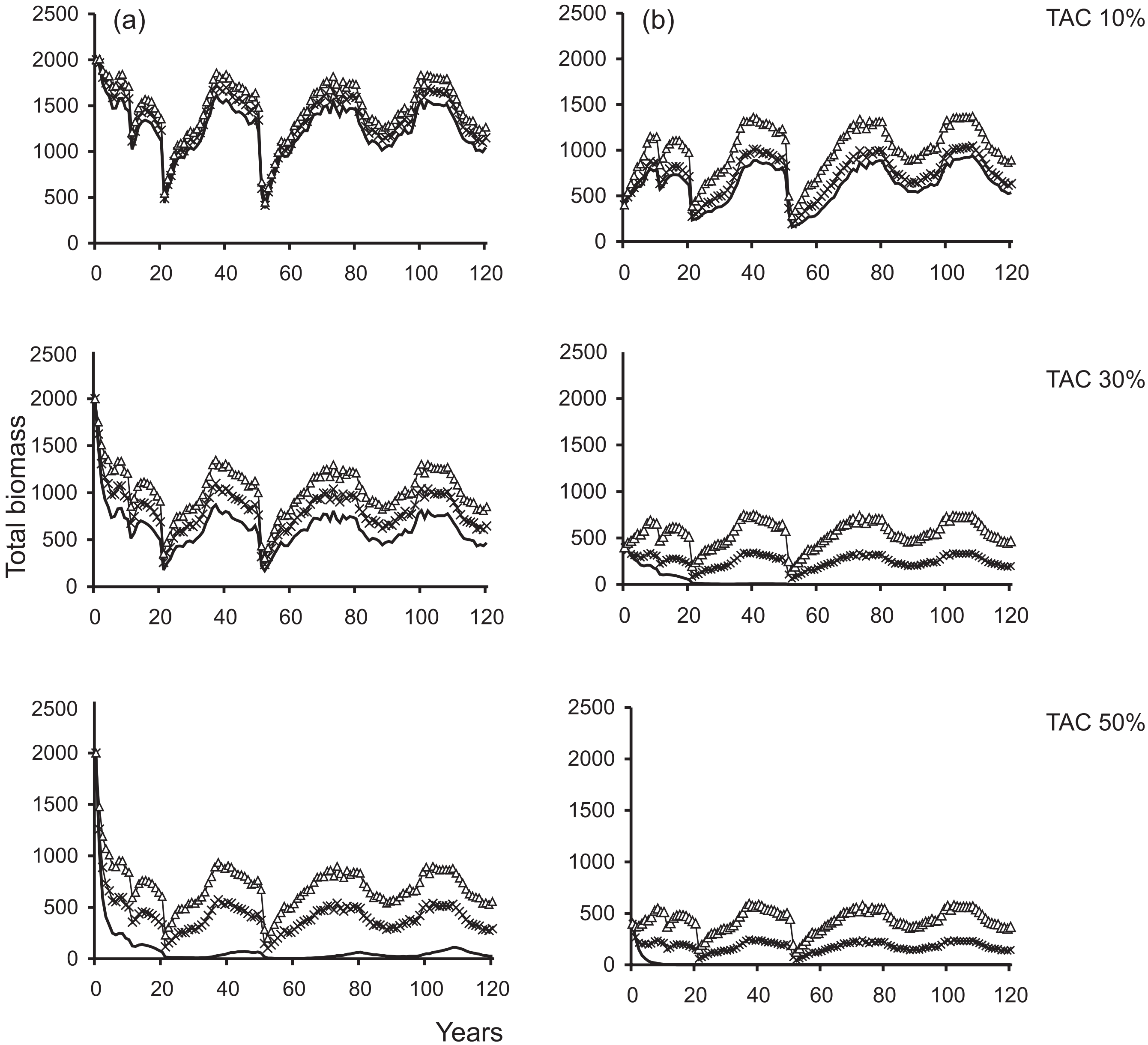
coverage of 40% of the management area can increase total biomass levels from the initial level of 400, but total biomass falls far short of the carrying capacity of the stock because of the prevailing high exploitation rate in the fishery (Fig. 4*b*).

How does the reserve affect the probability of achieving management biomass objectives?

For the open-access fishery, we present results for the deterministic and highly variable systems to compare probabilities of achieving target biomass levels stated in the management objectives (Fig. 5). Both deterministic and variable systems showed similar patterns of increasing probabilities with reserve coverage. We find that the probabilities of achieving target biomass level are slightly greater in the deterministic system, though for these target objectives, this is only evident in the previously unexploited stock. If the objectives were more risk averse, such as 60% of carrying capacity 60% of the time and 35% of carrying capacity 80% of the time, the probabilities of achieving each target biomass level would be significantly higher in the deterministic system. This is not surprising given that the natural mortality pulses in the variable conditions increase natural mortality rate. This does suggest, however, that ignoring such plausible events inherent in a variable environment may result in an overestimation of total biomass levels in a fishery. When the stock is initially at its carrying capacity, reserves greatly increase the probabilities of achieving even the highest target levels of biomass (Fig. 5*a*). For example, in a highly variable system, a 20% reserve coverage increases the probability of achieving 35% of carrying capacity (50% of the time) from 0 without a reserve to 1, whereas 40% reserve coverage would increase the probability of achieving 60% of carrying capacity (25% of the time) from 0 without a reserve to 1.

When the stock has previously been heavily exploited (Fig. 5*b*), it takes larger reserves to increase the probability of achieving target biomass levels. For example, in the highly variable system, it takes 40% reserve coverage before 35% carrying capacity is guaranteed (50% of the time) and 60% reserve coverage to guarantee 60% carrying capacity (25% of the time). This compares to 20% and 40% reserve coverage if the stock was previously unexploited. Without the reserve, the previously heavily exploited stock will collapse (i.e., the 5% carrying capacity objective is not guaranteed). If previously unexploited, however, there is a probability of 0.93 that 5% carrying capacity can be maintained (Fig. 5*a*).

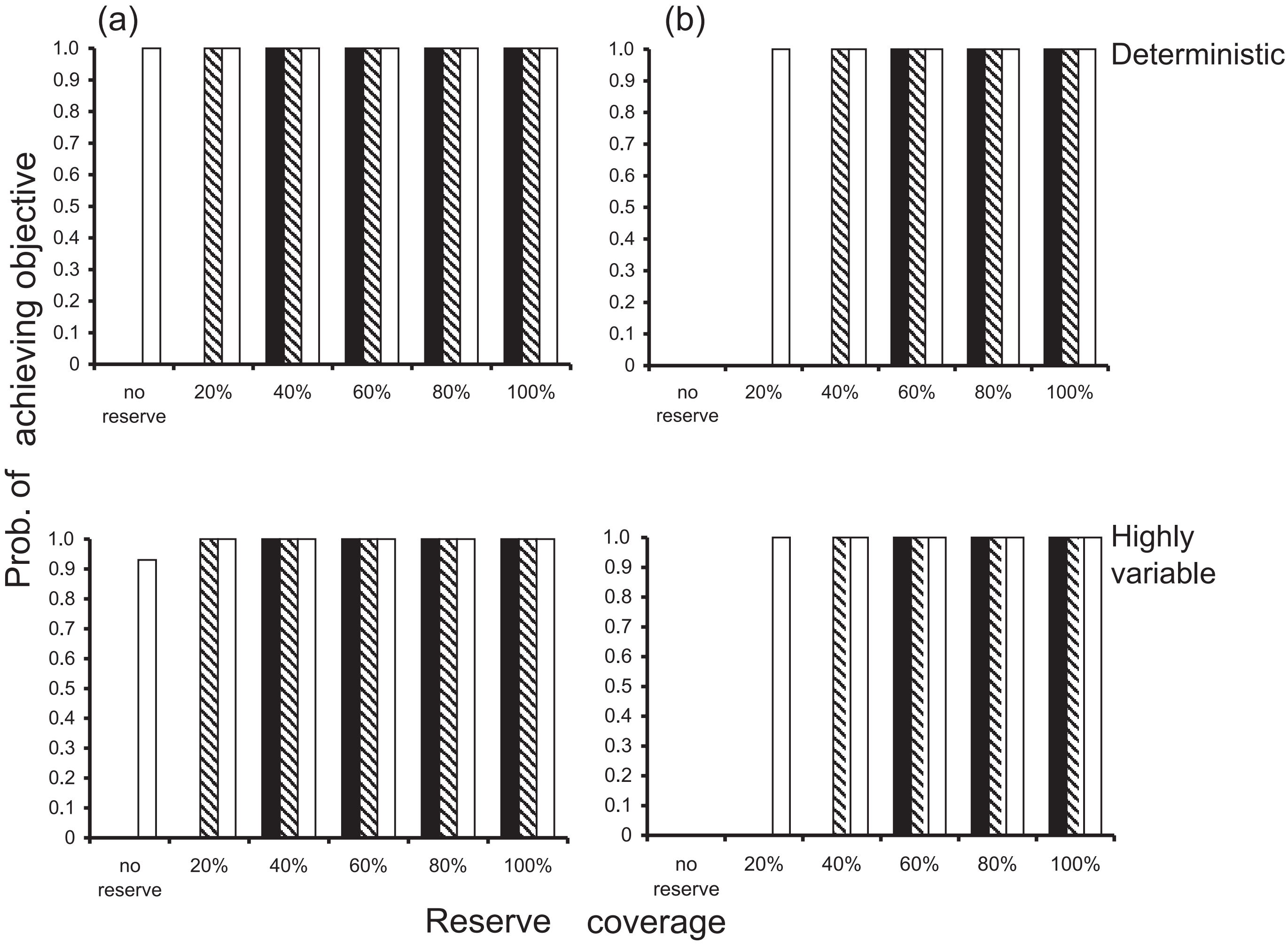
Fig. 4. Total biomass levels in a total allowable catch (TAC)-regulated fishery in a highly variable system, with TAC 10%, TAC 30%, and TAC 50% for (*a*) previously unexploited stock and (*b*) previously heavily exploited stock. No reserve (solid line), 20% reserve (×), and 40% reserve coverage (△) are shown. The figures represent one sample run (out of 200 runs).



In the TAC-regulated fishery, the probabilities of achieving target biomass levels are again increased with a reserve in most cases if the system is highly variable (Fig. 6). In the highly variable system at low levels of exploitation (TAC 10%), a previously unexploited stock can achieve all biomass objectives even without a reserve. If, however, the stock has previously been heavily exploited, a 20% reserve is required to guarantee the 35% carrying capacity objective and a 60% reserve to guarantee the 60% carrying capacity objective. The probabilities of achieving biomass management objectives generally decline as the TAC level increases to 30% and then 50%. However, with a previously exploited stock, the probabilities are the same for the TAC 30% and 50% case. With a TAC of 50%, a reserve coverage of 40% can only guarantee that the stock does not collapse (fall below 5% carrying capacity), 60% reserve coverage would guarantee the 35% carrying capacity objective is met, and 80% reserve would be required to achieve the 60% carrying capacity objective for both previously unexploited and heavily exploited stocks (Fig. 6).

It is worth noting that the management objective of achieving 60% carrying capacity (25% of the time) in a previously unexploited stock can be achieved by maintaining a low TAC of 10% in the whole fishing ground, by establishing 60% reserve coverage and allowing a TAC of 30% in the remaining (40%) fishing grounds, or by establishing an 80% reserve coverage and allowing a TAC of 50% in the remaining (20%) fishing grounds. In the case of a previously heavily

Fig. 5. Probabilities of achieving management objectives of target biomass levels in an open-access fishery in a deterministic and a highly variable system for a (*a*) previously unexploited stock and (*b*) previously heavily exploited stock for various coverages of marine reserves. 60% carrying capacity 25% of time, solid bars; 35% of carrying capacity 50% of time, hatched bars; and 5% of carrying capacity 100% of time, open bars.



exploited stock, the objective of preventing stock collapse (5% carrying capacity 100% of the time) can be achieved either by maintaining TAC of 10% in the whole management area or by allowing a TAC of 50% in 60% of management area (i.e., with a 40% reserve coverage).

Similar patterns of increasing probabilities with reserve size are found in the deterministic and variable systems, but in general the probability of achieving target biomass levels for all reserve sizes is higher in the deterministic system (as expected because of natural mortality pulses). This highlights the impact of variability on reducing the probability of achieving target biomass levels and reinforces the need for reserves to counter the effects of environmental variability.

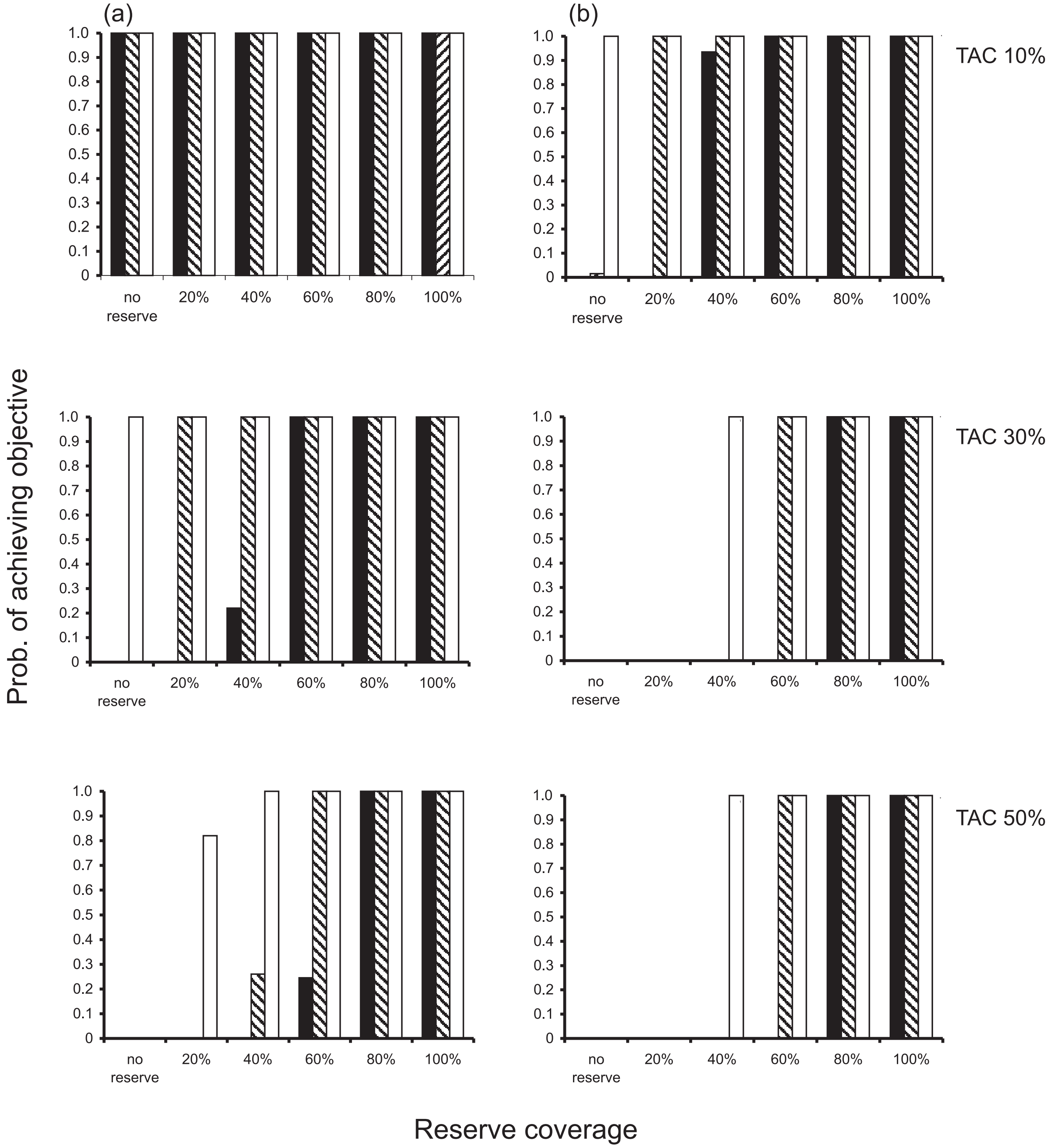
Impacts on catch

What is the impact of reserve establishment on the levels and variability of catches in the fishery?

In an open-access fishery, where the system is highly variable, if the stock is previously unexploited, the no-reserve case can produce higher mean catches than 20% and 40% reserve coverage (as seen in Fig. 7) but also more variable catches (Table 1). However, without a reserve, the trend in catch in both the deterministic and variable cases appears to be towards zero, whereas the 20% and 40% reserves appear to stabilize catches at a higher level towards the end of the time period (Fig. 7). Mean catches are approximately 159 (±50) without the reserve compared with 153 (±39) with 20% reserve coverage and 125 (±32) with 40% reserve coverage (Table 1). Percent variability (SD/mean catch × 100) is lower with the reserve (24%–26%) compared with without the reserve (31%) but does not decline uniformly with reserve size.

If the stock was previously heavily exploited, a reserve of 40% in the open-access fishery produces the highest catches of 59 (±17) compared with 18 (±9) of no reserve. Mean catches with reserve coverages up to 80% are higher than those without the reserve and in terms of percent variability are less variable (Table 1). If we take the percent variability as the measure of variability, the larger the reserve, the less variable the catches — ranging from 50% without the reserve to 26% with an 80% reserve. Furthermore, in the pre-

Fig. 6. Probabilities of achieving management objectives of target biomass levels in a total allowable catch (TAC)-regulated fishery in a highly variable system for fisheries regulated by TAC 10%, 30%, and 50% in (*a*) previously unexploited and (*b*) previously heavily exploited stocks. 60% carrying capacity 25% of time, solid bars; 35% of carrying capacity 50% of time, hatched bars; and 5% of carrying capacity 100% of time, open bars.

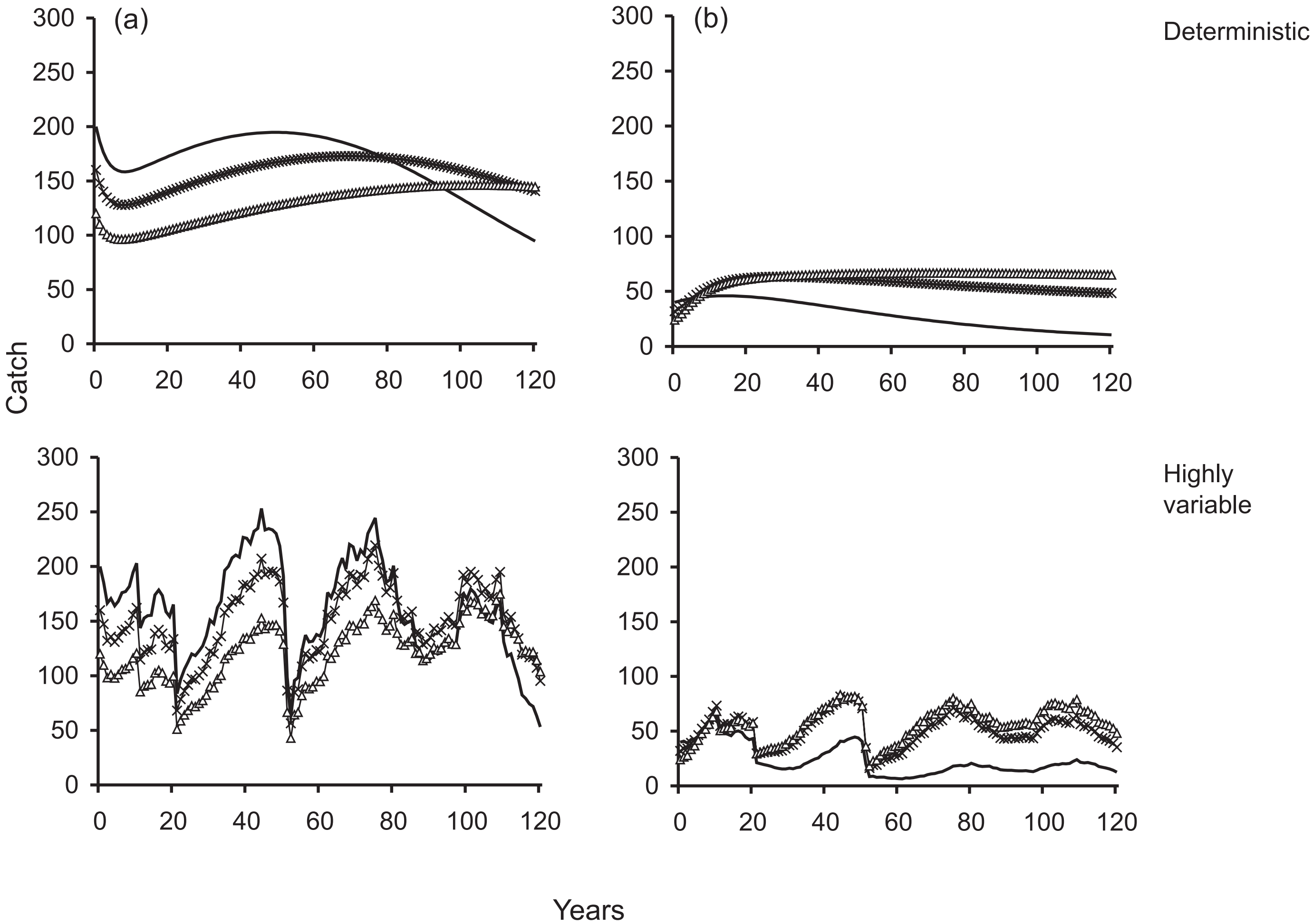


viously heavily exploited fishery, if there is no reserve, catches plummet to near zero levels by year 120 in both the deterministic and the variable systems (Fig. 7*b*).

In the TAC-regulated fishery (Fig. 8) with a previously unexploited stock, catches are higher with no reserve if the TAC is 10%, 20%, or 30%. For TACs of 40% and 50%, catches with the 20% reserve are higher and also less variable (Table 1). For example, mean catches with a TAC of 40% in a previously unexploited stock are 133 (±33%) without a reserve, 143 (±27%) with a 20% reserve, and 132 (±24%) with a 40% reserve. With a TAC of 50%, mean catches in a previously unexploited stock are 18 (±66%) without a reserve, 103 (±31%) with a 20% reserve, 114 (±26%) with a 40% reserve, and even 100 (±23%) with a 60% reserve.

If the stock has previously been heavily exploited, catches without the reserve fall to zero once the TAC is 20% or higher (Table 1). Therefore, reserves of 20%, 40%, 60%, and even 80% will produce higher catches under conditions of previous heavy exploitation combined with continuing moderate to heavy exploitation. Even for low TAC levels (TAC

Fig. 7. Catch levels in an open-access fishery for two stocks: (*a*) previously unexploited and (*b*) previously heavily exploited. No reserve (solid line), 20% reserve (×), and 40% reserve coverage (△) are shown for deterministic and highly variable systems.



10%), mean catches are higher with a 20%, 40%, and 60% reserve than without the reserve: 53 (±30%), 51 (±27%), and 41 (±27%) compared with 36 (±39%), respectively.

Sensitivity of results

We chose some of the parameters used in the previous analysis based on previous studies (e.g., reproductive capacity from Rodwell et al. 2002), the literature (natural mortality from Pauly and Ingles 1981), and others on what we believe are reasonable estimates (e.g., movement rates of fish and larvae). However, we accept that some of the outcomes of the analysis may be sensitive to some assumptions and parameter choices made. Two main assumptions are the movement rates of larvae and fish and the initial stock condition and growth rate.

Movement rates of larvae and fish

The nature of the movement of fish and larvae between a reserve and fishing ground is a common and important question and one with implications for reserve design and location. The case shown is a system with moderate fish movement and 50% larval retention. This was chosen as a middle ground, assuming that the reserve in question would export some fish and some larvae in response to changing biomass levels in the fishing ground and the reserve.

Clearly if the mobility of fish and larvae were significantly different from that assumed, the simulation results may be quite different. For example, if mobility were increased such that there is uniform larval dispersal ($\theta = 0$) and high fish movement ($\sigma = 1$), reserves are likely to produce higher catches than suggested, with a less dramatic reduction in catch variability. For example, for the case of a previously unexploited stock with a reserve coverage of 40% and TAC of 30% in the remaining fishing grounds, mean catches increased from 134 ± 30 to 152 ± 34 because of the higher movement rate. There may also be a lower probability of meeting biomass target levels because more of the biomass will be moving out of the protected area. Note that for the same example above, the probabilities of reaching each of the target levels remained unchanged.

If the system was closed, however, with complete larval retention ($\theta = 1$) and no fish mobility ($\sigma = 0$), the reserve will reduce mean catches, since there is no replenishment effect from the reserve to the fishing ground. For example, for the case of a previously unexploited stock with a reserve coverage of 40% and TAC of 30% in the remaining fishing grounds, mean catches decreased from 134 ± 30 to 105 ± 26 because of the lower movement rate. Catches are likely to be just as variable (in terms of percent) with or without the reserve because of the lack of spillover from the reserve pro-

Table 1. Mean catch levels with standard deviation (SD) and percent variability (var.) for previously unexploited and previously heavily exploited stocks for a highly variable system in an open-access and total allowable catch (TAC) quota fishery.

		Previously unexploited			Previously heavily exploited		
Fishery regime	Reserve coverage (%)	Mean	SD	% var.	Mean	SD	% var.
Open-access	No reserve	159	50	31	18	9	50
	20	153	39	25	50	16	32
	40	125	32	26	59	17	29
	60	82	21	26	50	14	28
	80	36	9	24	27	7	26
TAC (%)							
10	No reserve	121	26	21	36	14	39
	20	100	21	21	53	16	30
	40	78	17	22	51	14	27
	60	54	11	20	41	11	27
	80	28	6	21	24	6	25
20	No reserve	170	38	22	0	0	—
	20	146	32	22	44	14	32
	40	118	25	21	59	17	29
	60	84	18	21	54	14	26
	80	45	10	22	35	9	26
30	No reserve	175	43	25	0	0	—
	20	159	37	23	36	10	28
	40	134	30	22	56	15	27
	60	100	21	22	58	15	26
	80	55	12	21	40	10	25
40	No reserve	133	44	33	0	0	—
	20	143	38	27	33	9	27
	40	132	31	24	55	14	25
	60	104	23	22	60	14	23
	80	61	13	22	43	10	23
50	No reserve	18	12	66	0	0	—
	20	103	31	31	32	8	25
	40	114	29	26	55	13	24
	60	100	23	23	62	14	23
	80	62	14	22	46	10	23

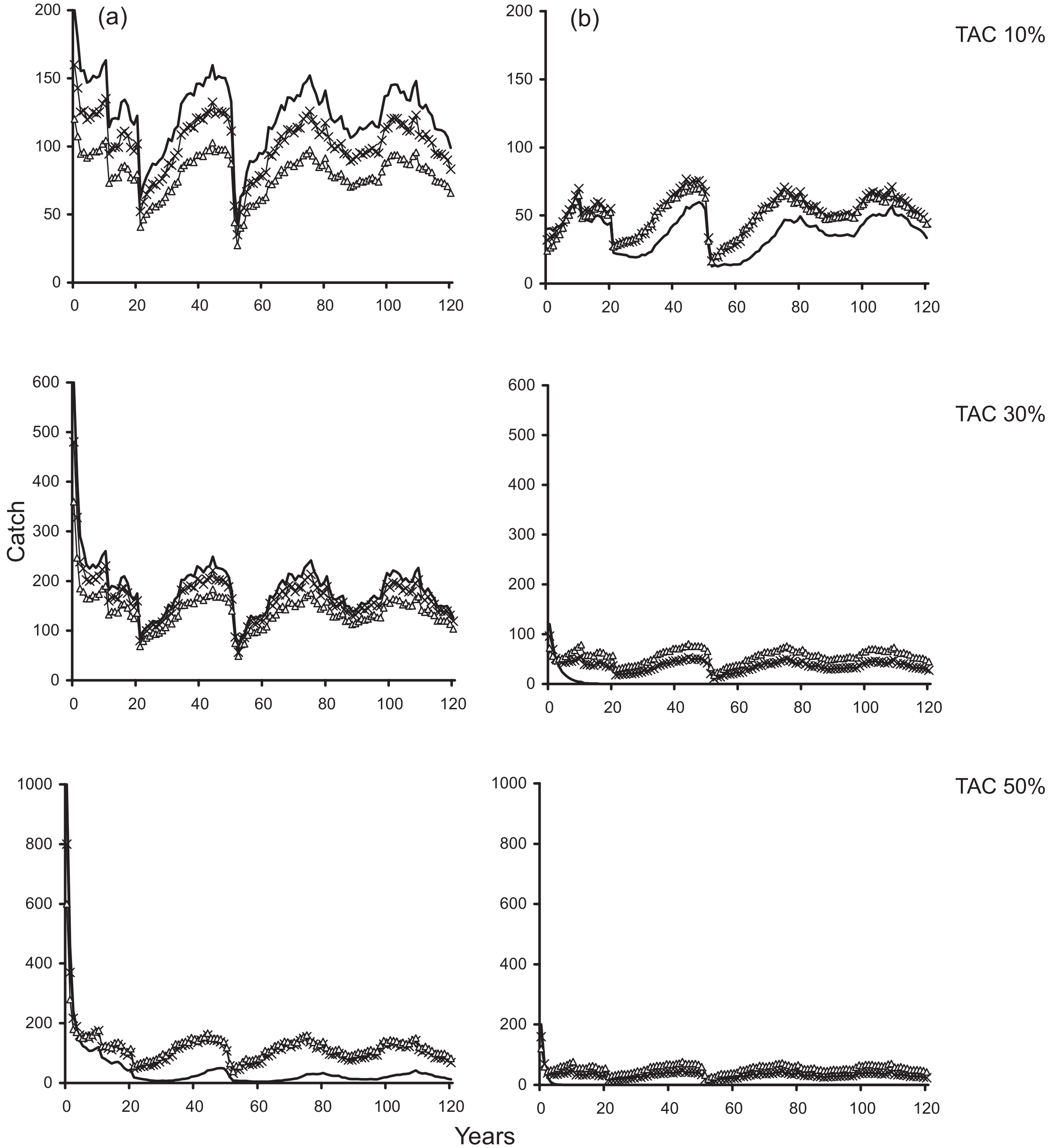
viding a stabilizing effect. The probability of achieving total biomass target levels may increase because part of the stock will be permanently protected. For the example above, the probability of reaching the target level of 60% carrying capacity (25% of the time) rose from 0.22 to 1. This extreme case of a closed system may occur if the reserve is sited around isolated habitat patches rather than in places where habitat is contiguous with fishing grounds.

In general, there must be bidirectional or source dynamics in order for reserves to feed fishing grounds (L.D. Rodwell, unpublished data). However, though alternative movement patterns, such as a reserve sink or lower fish and larval mobility, can reduce catch levels, catches are likely to still be less variable with a reserve if the fishery is heavily exploited.

Initial stock condition and growth rate

We have chosen two scenarios of initial stock condition. One is the extreme of an unexploited stock operating at carrying capacity, which is then subjected to fishery exploitation with or without a reserve. The second is taken as a heavily exploited stock at one fifth of its carrying capacity, which if left unexploited, would reach its carrying capacity after approximately 20 years. We take this to reflect a realistic scenario. However, if the previously heavily exploited stock were to grow at a slower rate, reaching the carrying capacity after 40 years if left unexploited (achieved by changing β to 2.5 and γ to 0.0007), catches would be much lower than recorded (Table 1). For example, with 40% reserve coverage and a TAC of 30%, catches would be as low as 6 ± 3 compared with 56 ± 15. Catches would still be zero without the reserve. We also found that if the stock were much slower growing, reserves must be much larger to increase the probability of achieving target biomass levels. For example, in a previously heavily exploited fishery with a TAC of 30% in fishing grounds, a 40% reserve can no longer prevent stock collapse. The reserve would have to be 60% of management area to prevent stock collapse and a 100% closure would be required to guarantee all biomass target objectives are met (previously 80% coverage would have met all three objectives). The more the exploitation rate exceeds the replenishment rate, the more extensive protection is required. The stock in this case requires a large refuge simply to survive. If the stock is faster growing, smaller

Fig. 8. Catch levels in a quota-regulated fishery with total allowable catch (TAC) of 10%, 30%, and 50% for two stocks: (*a*) previously unexploited and (*b*) previously heavily exploited. No reserve (solid line), 20% reserve (×), and 40% reserve coverage (△) are shown. Note different scales on *y* axes for each TAC level.



reserves will produce the same benefits. The stock is still able to replenish itself at a quicker rate than exploitation and so requires less protection.

Implications of other assumptions and parameter choices

The stocks described have reproductive capacities that reflect their condition: 0.7 (70% reproductive mature at carrying capacity) and 0.2 (20% reproductively mature if heavily exploited). These values are taken from Rodwell et al. (2002, 2003). We assume that if reproductive capacity remains at 0.2, the stock will not reach carrying capacity. Only if allowed to increase to 0.7 is this possible. Assumptions made about the relative reproductive capacity of reserve and fishing ground stocks can influence the relative effectiveness of reserves in increasing catches. For example, if $\varepsilon_1 = \varepsilon_2 = \varepsilon$ (i.e., reproductive capacity is uniform throughout management area), which is extremely unlikely in practice, then mean catches are more likely to be lower with the reserve.

In the simulations, recruitment in the fishing ground is assumed to be a function of fish biomass post-exploitation (i.e., all exploitation takes place before spawning ψ = 1). However, recruitment may take place before some or any exploitation occurs (i.e., $\psi = 0$ (no exploitation before spawning) or 0.5 (50% exploitation before spawning)). This may occur in a seasonal fishery. The timing of exploitation can have important implications, particularly in a regulated fishery. If a fishery operates in such a way as to allow recruitment to take place before exploitation, then the fishery can be more productive and there is less argument for a reserve on catch enhancement grounds. However, in reality the variability in recruitment patterns may make this type of regulation ineffective.

We considered years 21–120 as a 100-year period of analysis. This was designed to eliminate extreme adjustment periods and to concentrate more on the equilibrium results on catch, biomass, and variability. However, we did analyse the results for a 1- to 100-year period to check if this influenced the conclusions considerably. The probabilities of achieving target biomass levels remained unchanged for most reserve coverages and TAC or open-access cases. However, for a TAC of 10% in a previously heavily exploited stock, 40% reserve coverage had a probability of 0.94 of achieving the 60% carrying capacity objective if years 21–120 were considered but only 0.24 if years 1–100 were considered. This indicates the tendency for biomass to build up over time with reserve protection. Also, for both TAC and open-access regimes, catches for the no-reserve case were slightly higher and more variable if years 1–100 were considered (i.e., years 1–20 are those before catches responded fully to exploitation); catches with a reserve remained very similar, and the comparative catch status of reserve and no-reserve case remained unchanged. The time frame of 100 years was taken as realistic. However, some may view 20 or 50 years to be more realistic in management terms. The shorter the management time frame considered, the less favourable the reserve contributions would appear. Reserves produce long-term benefits. Therefore, the longer the management horizon, the more likely reserves are to be useful as management tools from both fishery catch and fish biomass perspectives.

Discussion

Reserves can increase the probability of achieving target biomass levels

The mean total fish biomass level was found to be higher with a reserve regardless of the initial condition of the stock, variability, or the fishery regime. Total biomass levels increased with reserve coverage. The probability of the stock remaining above target levels of biomass generally increased with the presence of the reserve in both deterministic and variable systems. The greater the reserve coverage and the better the initial condition of the stock, the greater the probability would be of reaching targets levels of fish biomass in the fishery.

The highly variable system had lower probabilities of reaching target biomass levels for most reserve scenarios and an increased chance of stock collapse in the absence of a reserve. However, the probability of achieving each target level was generally greater with a reserve than without, and probabilities increased as reserve coverage increased. If the stock had previously been heavily exploited, larger reserves may have been required to replenish stocks (i.e., sufficiently increase probability of attaining target biomass levels). The results of this study suggest, however, that once stocks have recovered, reserve coverage could be reduced without reducing the probability of maintaining target biomass levels (i.e., the stock moves from the state of previously heavily exploited to the state of previously unexploited after protection).

In a quota-regulated fishery with a high TAC, the reserve would have to be large to make a real difference to probabilities of attaining target stock levels. However, if the TAC were reduced, small reserves could substantially increase this probability. In each scenario, reserves showed the potential to eliminate the possibility of stock collapse even in a highly variable system.

Higher movement rates out of the reserve may reduce the probability of achieving target biomass levels, and lower movement may increase probabilities. The probability of achieving target biomass levels will also fall with the growth rate of the stock. Slower growing stocks will need larger reserves to achieve target biomass levels. The findings that reserves increase the probability of achieving target biomass levels and that they can prevent stock collapse in heavily exploited fisheries are sound regardless of the assumptions regarding reproductive capacity of reserve and fishing ground stocks, recruitment timing, or movement patterns. The reserve coverage required to achieve this objective, however, increases with exploitation rate in the remaining fishery.

Reserves can enhance mean catches in a fishery over time

Mean catches can be enhanced with a reserve, but the biological and economic conditions in the fishery will determine at what level of exploitation reserves will enhance catches and what coverage reserves need to achieve this objective. We can say that the higher the exploitation rate in the fishery, the more likely that catches will be enhanced by the presence of a reserve but only if there is some moderate movement of larvae and (or) fish out of the reserve. In closed systems, reserves will clearly not enhance catches.

If the stock has previously been unexploited (or experienced low exploitation), the establishment of the reserve may lead to lower catch levels than with the no-reserve case. This will depend on the fishery regime. Open-access results show lower mean catches with reserves. In the quota-regulated fishery, if TAC remains low then mean catches will again be lower with reserves. As the TAC increases, mean catches with small reserve coverage can exceed mean catches without the reserve. Even large reserve coverage could produce greater catches than catches without a reserve if the stock has previously been heavily exploited. In the open-access fishery, the effectiveness of the reserve in enhancing catches is highly dependent on the condition of the stock prior to protection. This may be explained by the fact that under conditions of open access, a previously heavily exploited stock will not have the opportunity to recover to levels at which catch can be enhanced (unlike a fishery regulated by strict quotas). However, in a quota-regulated fishery, the TAC levels would have to be high for a small reserve coverage to increase mean catches. These results are consistent with other modelling efforts that suggest that marine reserves will enhance catches in heavily exploited fisheries (e.g., Holland and Brazee 1996; Sanchirico and Wilen 2001; Rodwell et al. 2003).

In an open-access fishery, mean catches with a reserve were only higher in the case where the stock was previously heavily exploited. In a quota-regulated fishery, a small reserve coverage could prevent fishery catches from collapsing completely, even when the TAC was set high, regardless of the previous condition of the stock or high level of variability. Given that in the 1980s and 1990s in the North Sea, 2- to 8-year-old cod (http://www.cefas.co.uk/fsmi/roundfish-cod.htm) and 2- to 6-year-old haddock (http://www.cefas.co.uk/fsmi/roundfish-haddock.htm) were estimated to be exploited at a rate of approximately 50%–60%; our results support the suggestion that collapse of these stocks may be imminent in the absence of reserve protection or effective measures in fishing effort reduction.

Higher movement rates from the reserve increased the mean catch levels in the fishing ground, and lower movement reduced mean catches. Mean catches will be lower if the growth rate of the stock is slower than simulated for the previously heavily exploited stock.

Reserves can reduce the variability of catches in the fishery

Depending on the initial condition of the stock and the fishery regime in place, reserves can reduce the variability of catches. In general, we found that if the stock was previously unexploited in an open-access fishery, the level of variability (in terms of percent variability) declined with reserve coverage. This was also true in a quota fishery with moderate to high TAC levels. However, if TAC levels were low, the levels of variability were not significantly different with or without the reserve.

If the stock had been previously heavily exploited variability, in catches declined with reserve coverage. However, for a fishery with moderate to high TACs, catches without the reserve were zero and so stable. Therefore, we conclude that even in a highly variable system, reserves can reduce variability of catches if the fishery is moderately to heavily exploited, a finding consistent with those of Mangel (2000*a*, 2000*b*) and Pezzey et al. (2000). Under some conditions (e.g., low exploitation), mean catches can be reduced because of reserve establishment resulting in a mean–variance trade-off (e.g., Dixit and Pindyck 1994). It may be desirable in some fisheries to accept lower catches in return for more predictable catches.

Lower levels of fish or larval movement will reduce the impact of the reserve on variability. In the extreme case of a zero movement rate, we found that percent variability with or without the reserve was the same. The movement of fish and larvae from the reserve can have a stabilizing effect on the catches in the fishing ground. If growth of the stock is slower, the catches are likely to be lower and perhaps more variable in term of percentage. However, the results for catch variability are not conclusive for very slow-growing stocks.

Two fishery regimes compared

Although in general, results were similar between open-access and quota management regimes, there were some notable differences. Firstly, the open-access fishery did not collapse completely in the time period tested, but in the quota fishery, the stock could collapse after as little as 10 or 20 years. This suggests that under open-access conditions, the stock is able to bounce back from low biomass levels because of a reduction in fishing effort. However, in reality these low levels of biomass may be insufficient for some species to recover. Secondly, we assume that fishing effort has a reasonably high response. High capital investment in boats and fishing gear may in fact make fishing effort less flexible than assumed. In the quota fishery, even if biomass drops to critical levels, a proportion will still be removed. If quotas are set too high (because of lack of knowledge of stock condition, for example), the stock can collapse. High levels of exploitation in an open-access fishery may be due in part to government subsidies making fishing costs artificially low. High quotas may arise from politicians seeking to avoid economic hardship that lower quotas might entail.

The danger of setting quotas based on estimates of biomass is clear. The quotas are a fixed proportion of biomass, but the stock is variable. In a quota fishery, there is a far greater danger of stock collapse without a marine reserve. As noted previously, reserves of between 20% and 40% have been suggested by scientists as the range needed to assure fishery benefits (Roberts and Hawkins 2000; NRC 2001; Gell and Roberts 2003). This recommended range of reserve coverage as a tool to prevent stock collapse is supported by the findings of this study, though we acknowledge that the conditions in each fishery will require individual consideration. Larger reserves would create greater buffers but may result in lower catches. Furthermore, we find that a very slow-growing stock may require full protection from fishing if previously heavily exploited.

The variability and uncertainty of marine environments strengthens the argument for marine reserves as refuges from exploitation. This study supports others that suggest that the presence of fully protected marine reserves can insure against stock collapse (Lauck et al. 1998; Mangel 2000*a*). Reserves could increase the ability of fishery managers to achieve target levels of biomass, particularly in variable environments, and reduce the variability in catches in neighbouring fisheries, making future planning in the fishery more efficient. In heavily exploited fisheries, reserves are also likely to enhance mean catches so long as fish and (or) larvae are moderately mobile.

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